SYMBIOSIS AS AN EVOLUTIONARY INNOVATION IN THE RADIATION OF PLANKTIC FORAMINIFERA

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Symbioses have been considered an important means for the creation of evolutionary novelty as well as a trigger for the abrupt appearance of higher taxa. The union between two different genomes can equip the partners to diversify into habitats previously unavailable to one or both of the symbionts and lead to taxonomic radiation as the symbionts enter a new adaptive zone. Symbioses might also be expected to play a role in the maintenance of high diversities or species longevities by initially relaxing competition with non-symbiotic sister taxa and promoting the survival of daughter species. Presumably, radiation should continue until the symbiotic partners fill the array of habitats opened to them by their newly acquired body plan and ecology. Hence, the macroevolutionary effects of symbiosis may include both the initial diversification of at least one of the symbionts followed by continued high rates of morphological and ecological radiation.

Planktic foraminifera frequently form symbiotic associations with algal protists. The symbiosis is obligate for many foraminifer species and appears to permit their growth and reproduction in nutrient-depleted surface waters such as the blue water, 'biological deserts' of the subtropical oceanic gyres. Modern photosymbiotic foraminifera tend to be more cosmopolitan in their distributions than non-symbiotic species and there is experimental evidence that symbiotrophs have longer survival times under conditions of nutrient stress than asymbiotic taxa. Furthermore, it is possible to detect the signature of symbiosis in extinct foraminifera through distinctive isotopic cues preserved in the foraminifer's calcareous shell.

The fossil record of foraminifer-algal symbiosis suggests that the appearance of this ecological association contributed to the timing of radiation in Paleocene planktic foraminifera. Isotopic evidence shows that photosymbiosis evolved in synchrony with a major diversification of trochospiral planktic foraminifera about 3.5 my after the end-Cretaceous extinction. The simultaneous taxonomic radiation and acquisition of photosymbiosis is evidence that the ecological strategy permitted foraminifera to expand their niche in pelagic environments by diversifying into low nutrient surface waters.

A comparison of the species longevities of Neogene and Paleogene symbiotic clades suggests that photosymbiosis does not regulate the characteristic rate of taxonomic turnover in clades after they appear. Photosymbiotic clades are not geologically longer-ranging than asymbiotic clades. Likewise, there are no specific morphological characteristics that are consistently associated with photosymbiosis when the various photosymbiotic clades of foraminifera are considered as a group. Symbiotic foraminifera display a large array of shell morphologies even among living species that include spherical, globular-spinose, globular non-spinose, keeled non-spinose, and planispiral shell morphologies. Hence, if symbiosis did contribute to the taxonomic radiation of foraminifera it did not also govern either the details of morphologic evolution within these groups after they appeared or their characteristic species diversity. Symbiosis may provide more of a jump-start for diversification by opening new evolutionary opportunity than a motor driving the evolutionary machine.

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